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The importance of localized culling in stabilizing chronic wasting disease prevalence in white-tailed deer populations

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ABSTRACT

Strategies to contain the spread of disease often are developed with incomplete knowledge of the possible outcomes but are intended to minimize the risks associated with delaying control. Culling of game species by government agencies is one approach to control disease in wild populations but is unpopular with hunters and wildlife enthusiasts, politically unpalatable, and erodes public support for agencies responsible for wildlife management. We addressed the functional differences between hunting and government culling programs for managing chronic wasting disease (CWD) in white-tailed deer by comparing prevalence over a 10-year period in Illinois and Wisconsin. When both Illinois and Wisconsin were actively culling from 2003 – 2007, there were no statistical differences between state CWD prevalence estimates. Wisconsin government culling concluded in 2007 and average prevalence over the next five years was $3.09 \pm 1.13\%$ with an average annual increase of 0.63%. During that same time period, Illinois continued government culling and there was no change in prevalence throughout Illinois. Despite its unpopularity among hunters, localized culling is a disease management strategy that can maintain low disease prevalence while minimizing impacts on recreational deer harvest.

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1. Introduction

North American cervids [mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*)] are popular game animals making them economically and recreationally valuable species. Free-living cervids are susceptible to chronic wasting disease (CWD) (Miller et al., 2000; Spraker et al., 1997), a contagious and fatal prion disease

with no cure or treatment (Williams et al., 2002). To date, CWD has been identified in free-ranging cervid populations in 17 states and two Canadian provinces (<http://www.nwhc.usgs.gov/disease-information/chronic-wasting-disease/index.jsp>). CWD is spread in free-living animals through contact with bodily secretions or infectious agents persisting in contaminated environments (Mathiason et al., 2009, 2006; Walter et al., 2011; Williams et al., 2002). Such transmissibility results in a self-sustaining CWD epizootic with prevalence increasing slowly over time (Miller et al., 2000; Miller and Conner, 2005; Saunders et al., 2012; Williams et al., 2002). Furthermore, the environmental load of infectious prions increases with the number of infectious animals making CWD exceedingly difficult to eliminate from free-ranging populations once established (Almberg et al., 2011; Gross and Miller, 2001). CWD models suggest substantial

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declines in cervid populations with high prevalence and highlight the importance of long-term, sustained management programs in controlling CWD (Gross and Miller, 2001; Mateus-Pinilla et al., 2013; Wasserberg et al., 2009).

Information on CWD transmission dynamics in wild populations is very limited. A lack of data has resulted in uncertainty about management actions (Peterson, 1991; Wasserberg et al., 2009). The large number of stakeholders (including hunters, deer biologists, environmental interest groups, and the general public) increase the complexity of decision-making when dealing with threats to economically important agriculture commodities (Carstensen et al., 2011), human health (Daszak et al., 2000), environmental health and the conservation of native plant and animal species. State wildlife agencies are faced with the challenging task of managing deer herds for multiple objectives such as maintaining hunter opportunities, controlling disease spread, limiting negative deer–human interactions and conserving natural resources. Such conflicting objectives make best management practices for wild deer populations highly situational (Carstensen et al., 2011). Because neither practical vaccines nor treatments are available for CWD, reducing deer densities through culling is a common yet controversial disease management approach to minimize contact between infected and susceptible hosts (Carstensen et al., 2011; Potapov et al., 2012; Schmitt et al., 2002; Wasserberg et al., 2009). This practice has been important in successfully eliminating bovine tuberculosis from free-ranging deer in Minnesota (Carstensen et al., 2011) but at this time it is unclear to what extent culling controls CWD and to what extent culling affects hunter opportunity in CWD infected areas (Wasserberg et al., 2009).

CWD was first detected in Illinois and Wisconsin in 2002. Both states banned translocation and baiting of deer in CWD areas but responded with independent disease management strategies. The Illinois Department of Natural Resources (IDNR) implemented a disease management program to bring about small scale population reductions in known CWD infected areas by incorporating additional hunting seasons and government culling (Barlow, 1996). Culling was selective, only occurring in specific 64 km² sections [based on the Public Land Survey System (United States Department of the Interior, 2011)] where CWD had been detected by testing hunter-harvest deer. This approach focused culling on localized areas containing deer at greatest risk of current infection and future transmission to additional individuals while limiting the overall number of deer killed.

The Wisconsin Department of Natural Resources' (WDNR) CWD management program aimed at eradicating CWD from the state by establishing a disease management zone consisting of a 1064.5 km² area of complete deer eradication surrounded by herd reduction zones (Holsman et al., 2010; VerCauteren and Hygnstrom, 2011). Toward this goal, the WDNR began widespread government culling and attempted to increase hunter harvest opportunities despite declining hunter participation. In 2007, the WDNR culling program was greatly reduced because of public resistance and declining legislative support (Holsman et al., 2010; VerCauteren and Hygnstrom, 2011). Since then, Wisconsin

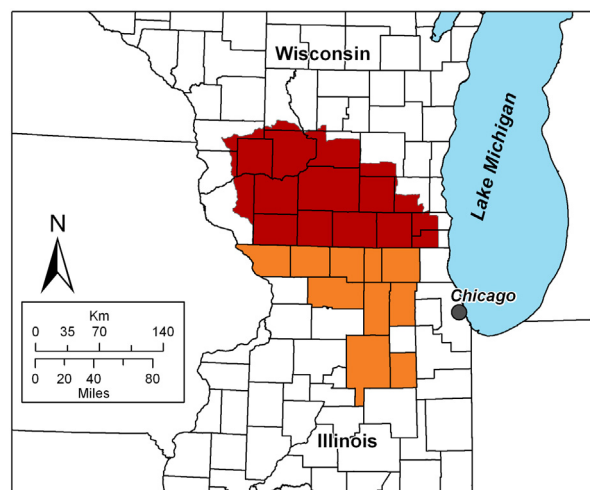


Fig. 1. Areas in Illinois and Wisconsin with chronic wasting disease detected over fiscal year 2003–2012. Orange areas are counties in Illinois and red areas are Wisconsin deer management units that were included in prevalence calculations.

has shifted from a government culling disease management strategy to controlling CWD primarily through public hunting (*Wisconsin's Chronic Wasting Disease Response Plan: 2010–2025*, 2010), while Illinois has consistently used localized government culling to control CWD for the past 10 years.

Public opposition to culling as a disease management strategy necessitates an analysis of a sustained culling program that would help guide agencies in selection of CWD management options. Our objectives were to determine if CWD prevalence was affected by the shift in disease management strategies between IL and WI in 2007 and to determine if hunting opportunities in the state of Illinois, where the management has been consistent over 10 years, were affected by disease management strategies.

2. Methods

Samples tested for CWD originated from both public hunting and government culling. All IL samples were tested by the Illinois Animal Disease laboratories using the gold standard immunohistochemical (IHC) examination of retropharyngeal lymph nodes and obex tissue samples. WI samples were tested by the WI Veterinary Diagnostic Laboratory using IHC, or an ELISA based screening test where positive samples were confirmed by IHC. The location of harvest was known for all tested deer samples at either section level or deer management units in IL and WI respectively. Both spatial resolutions met the geographical needs of our selected study area.

To determine whether CWD prevalence was affected by differing disease management strategies between both states, we evaluated 10 years of CWD test results from Illinois and Wisconsin. We calculated CWD prevalence as the number of positive deer divided by the number of total deer tested annually. We confined our prevalence calculations to those areas where CWD positives have been detected from 2002 to 2012 (Fig. 1). For

Table 1

Annual number of samples tested for chronic wasting disease based on Illinois Department of Natural Resources publically reported disease reports (dnr.state.il.us/cwd/) and Wisconsin Department of Natural Resources test results (dnr.wi.gov/topic/wildlifehabitat/results).

	Illinois	Wisconsin
2003	1,905 (14)	19,075 (205)
2004	3,841 (51)	13,330 (117)
2005	3,695 (31)	18,669 (145)
2006	3,900 (51)	19,564 (181)
2007	4,774 (42)	19,951 (205)
2008	5,142 (38)	7,175 (135)
2009	4,215 (30)	6,194 (181)
2010	3,553 (37)	6,916 (179)
2011	3,854 (42)	7,044 (219)
2012	4,465 (36)	4,871 (240)
Total	39,344 (372)	122,789 (1807)

Numbers of CWD positive deer are in parentheses.

Illinois, prevalence was based on information provided by the IDNR and available in the annual chronic wasting disease reports (<http://dnr.state.il.us/cwd/>). Positives have been detected in ten contiguous counties encompassing 15,786 km² (Boone, DeKalb, Grundy, Jo Daviess, Kane, LaSalle, McHenry, Ogle, Stephenson and Winnebago; Fig. 1). In the 10 years since CWD detection, 39,344 deer were tested in this part of Illinois (Table 1). To determine prevalence in Wisconsin, we used publically reported test results downloaded on September 8, 2012, from <http://dnr.wi.gov/topic/wildlifehabitat/results.html>. Wisconsin data were reported from deer management units within the 22,878 km² disease management zone in southern Wisconsin where CWD positive deer have been found since 2002 (Fig. 1). These areas were specified by a CWD identifier (e.g. 29A-CWD). In the 10 years since CWD detection, 122,789 deer were tested in this part of Wisconsin (Table 1). Although sampling intensity varied across the two states areas, prevalence estimates using the smallest number of deer tested per year resulted in a 96% power to detect a 1% change in prevalence between both states within a single year (SPSS Sample Power v.2, Chicago, IL).

Wisconsin test results were reported in CWD years (April 1 through March 31) such that samples collected in the 2011 CWD year were collected between April 1, 2011, and March 31, 2012. Because Illinois results were reported in fiscal year (FY; FY 2012 samples were collected between July 1, 2011, and June 30, 2012), we matched each Wisconsin CWD year to the respective Illinois FY for parallel prevalence comparisons between states. For example, Wisconsin's 2011 CWD year was compared to that of Illinois FY 2012. Government culling as a management tool occurred in Illinois from 2003 until 2012 and in Wisconsin from 2003 until 2007. We evaluated culling as a management strategy using a generalized linear model (Proc GLM) with prevalence as a dependent variable and state, fiscal year, percent forest cover and percent clay as independent response variables. All interactions with state also were included in our initial model. Only predictors showing an association at a significance of 0.05 were included in the final models. All statistical analyses were performed in SAS v.9.3 (Cary, NC). Assumptions of homoscedasticity, normality and independence of residuals were evaluated through visual inspection of residual plots.

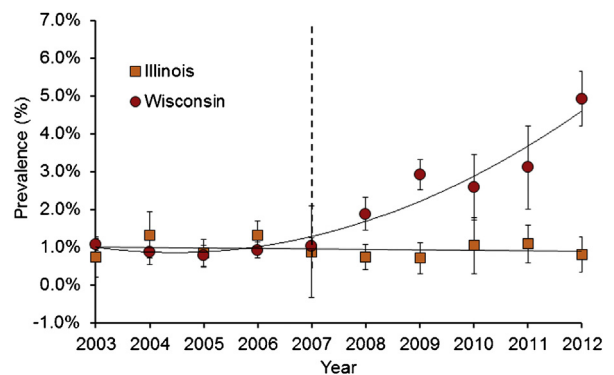


Fig. 2. Annual chronic wasting disease prevalence in Illinois and Wisconsin. Prevalence calculated as the total number of positive deer divided by the total number of deer tested (% ± SE). Illinois data obtained from annual chronic wasting disease reports downloaded from <http://dnr.state.il.us/cwd/>. Wisconsin data was downloaded on September 8, 2012 from <http://dnr.wi.gov/topic/wildlifehabitat/results.html>. Dashed line indicates last year of extensive government culling throughout the Wisconsin disease management zone by WDNR.

To determine if annual variation in Illinois hunter success has been affected by CWD management, we used statewide hunter harvest data provided by the IDNR and downloaded on September 4, 2012 from <http://www.dnr.illinois.gov> and compared areas with and without government culling. All hunter harvest numbers were reported in fiscal year. We divided the state into three similarly sized analytical regions (approximately 48,500 km²). We used these three regions to compare average annual hunter harvest in the 10 years prior to (FY 1993–FY 2002) and 10 years post (FY 2003–FY 2012) state agency management implementation. Differences in hunter harvest within regions were tested using a generalized linear model. Initial predictors included region, time period and fiscal year as independent class variables with all interactions. Only predictors showing an association at a significance of 0.05 were included in the final models. We also evaluated statewide trends in public hunter harvest using the number of deer harvested in each region for the last 20 years calculated as a 3-year moving average (FY ± 1 year). Temporal trends within each region in hunter harvest were assessed using a generalized linear model with fiscal year as the independent response variable. Differences between regions were evaluated with fiscal year as a covariate and *post hoc* Tukey's tests.

To address effects of government culling at a more localized scale, we compared hunter harvest pre- and post-management in the ten counties where CWD has been detected (Fig. 1) as well as in the four counties where CWD management has been the longest and most intense (Boone, DeKalb, McHenry, Winnebago). We tested effects of government culling on public hunter harvest in these counties using a generalized linear model as previously described for regional differences.

3. Results

Annual CWD prevalence in Illinois has remained relatively flat since culling began in 2003 with an average

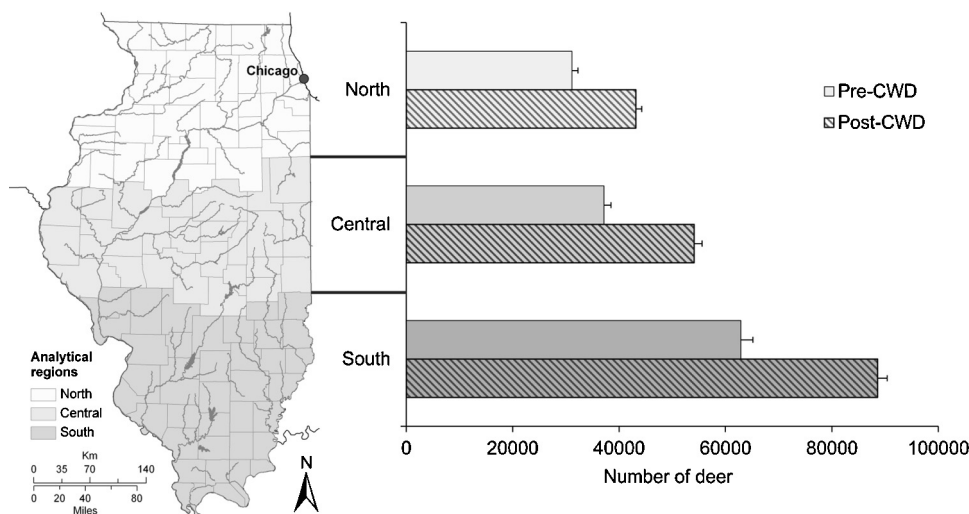


Fig. 3. Public hunter harvest of white-tailed deer throughout the state of Illinois. (Left) The state of Illinois was divided into three arbitrarily assigned analytical regions all containing similarly sized areas (approximately 48,500 km²). All counties with CWD positive deer fall in the North analytical region and additional deer seasons occurred only in this region. (Right) Average hunter harvest (mean \pm SE) in the 10 years pre- and 10 years post-CWD control implementation. Pre-CWD measured from fiscal year 1993 to 2002, post-CWD from fiscal year 2003 to 2012. All three analytical regions have showed significant increases in hunter harvest since CWD was detected in 2002.

annual prevalence of $0.95 \pm 0.23\%$ ranging from a low of 0.71% to a high of 1.33% (Fig. 2). Annual CWD prevalence within the Wisconsin disease management zone was stable during periods of CWD control incorporating government culling (2003–2007) but rose thereafter (Fig. 2). During the culling period, average annual prevalence in Wisconsin was $0.94 \pm 0.12\%$. When both Illinois and Wisconsin were actively culling from 2003 to 2007, there were no statistical differences between state CWD prevalence estimates. Wisconsin government culling concluded in 2007 and average prevalence over the next 5 years was $3.09 \pm 1.13\%$ with an average annual increase of 0.63%. During that same time period, Illinois continued government culling and there was no change in prevalence throughout Illinois. From 2008 to 2012, not only was average prevalence significantly greater in Wisconsin compared to Illinois ($F = 66.1$, $P < 0.001$) but the slopes suggest that the difference grew larger with time (Fig. 2). Despite differences between the states in percent clay (IL = 17.02%, WI = 13.06%) and percent forest cover (IL = 0.10%, WI = 0.32%), these variables were not retained in the model. Significant predictors of prevalence included fiscal year, state and the interactions of fiscal year and state, and percent forest and state.

We found greater public hunter harvest in the 10 years since culling began compared to 10 years pre-culling in all three regions throughout Illinois ($F = 40.1$, $P < 0.001$; Fig. 3) regardless of whether government culling occurred in the region. Hunter harvest increased over the past 20 years across the state (all regions: $r^2 = 0.87$, $P < 0.001$; Fig. 4). Based on the 3-year moving average over the past 20 years, deer harvest was lowest in 1992 (FY 1991–FY 1993) and greatest in 2007 (FY 2006–FY 2008) in all three regions. The number of deer harvested differed significantly by region ($F = 1925.7$, $P < 0.001$). Deer harvest was greatest in the south and least in the north (Tukey's *post hoc* test $\alpha = 0.05$).

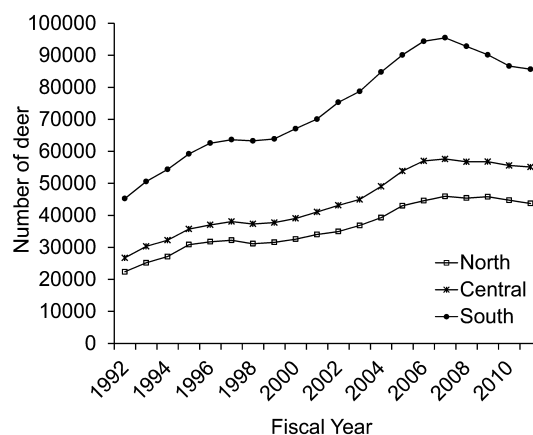


Fig. 4. Public deer hunter harvest trends from Illinois. Hunter harvest from north, central and south regions of Illinois using a 3-year moving average calculated as the average of each fiscal year ± 1 year. North, central and south regions are shown in Fig. 3.

The observed increase in hunter harvest within each region was consistent throughout the entire state.

Although harvest increased in the northern region after implementation of culling for CWD control, management only occurred in specific sections so it was important to evaluate changes in hunter harvest at a smaller scale. The Illinois disease management program has removed an average of 747 deer per year (range: 181–1203) from the ten counties where CWD has been detected since 2002. This removal represents 4.9% of the approximately 15,000 deer removed from those ten counties during each hunting season and has not resulted in a reduction in overall hunter harvest in those counties. When comparing the 10 years prior to CWD management to the 10 years since management began, significantly more deer were harvested from

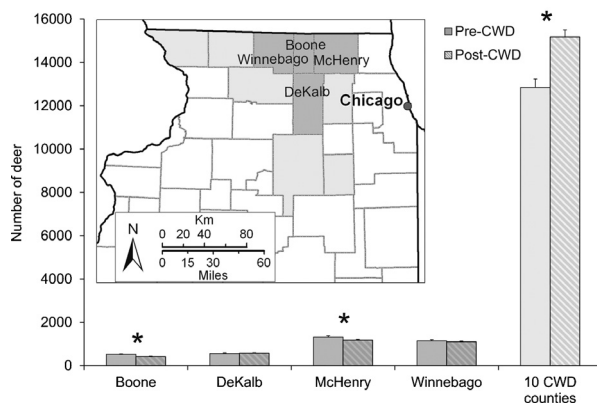


Fig. 5. Comparison of average annual public hunter harvest before and after implementation of CWD control program in Illinois. Average hunter harvest (mean \pm SE) in the 10 years pre- and 10 years post-CWD control implementation from the four CWD counties with 9–10 years of state agency management (inset: dark gray) and the ten counties combined where CWD has been detected in the last decade (inset: all shaded counties). Pre-CWD measured from fiscal year 1993 to 2002, post-CWD from fiscal year 2003 to 2012. Significant differences indicated by asterisks.

those ten counties in the latter years ($F = 276.2$, $P < 0.001$; Fig. 5); average annual hunter harvest increased by 18.1%.

Overall, government culling occurred in ten counties but the majority of the deer removed by the IDNR for CWD control were from four counties where CWD management has been ongoing for the last 9 (DeKalb) to 10 years (Boone, McHenry and Winnebago). At this smaller scale, two of the four counties had a significant reduction in hunter harvest between the 10 years prior to CWD control and the 10 years post CWD control implementation (Fig. 5). Average annual hunter harvest was reduced by 20.9% in Boone ($F = 7.4$, $P = 0.014$) and by 11.2% in McHenry ($F = 4.6$, $P = 0.045$); presence of culling was the only significant predictor. There have been no changes in hunter harvest in DeKalb and Winnebago counties.

4. Discussion

Although culling is a widespread strategy for wildlife disease management and for control of invasive animal species (Carstensen et al., 2011; Heberlein, 2004; Woodroffe, 1999), based on the results of our study the effectiveness of using public hunting rather than government culling is questionable. Reduction in local deer densities by IDNR contributed to a stable prevalence of $\sim 1\%$ over the last 10 years. Because culling in Illinois always occurs in areas with CWD, no experimental control area exists to statistically address the effect of not culling. However, comparison of prevalence in northern Illinois with publically available data for southern Wisconsin allows us to infer the association between different approaches to disease management and reduced CWD control in geographically similar areas. From 2003 to 2007, WDNR had a government culling program similar to Illinois and comparable CWD prevalence of 1%. In 2007, public pressure resulted in a severe reduction of Wisconsin's culling program. In the following 5 years, while Wisconsin relied

primarily on public hunting to reduce deer populations and control CWD, there was a steady increase in prevalence to a current level of almost 5%. The rise in prevalence of CWD in Wisconsin suggests that this disease cannot be contained effectively through hunter harvest alone. Over the same time period, the comparison of prevalence to Illinois suggests that culling effectively maintained low CWD prevalence.

Over the 10 years of this study, the primary factor included in this study that changed between the two states was management. While it is possible that the difference seen in prevalence between states is a reflection of differences in factors that affect disease transmission (e.g. forest cover) (Storm et al., 2013) or persistence of prions in the environment (e.g. clay, (Walter et al., 2011)), these factors did not explain the temporal differences we observed. We have no reason to suspect that forest cover and soil composition would change over the time of this study. The single factor of those examined in this study that we have identified that has changed in WI was the cessation of the sharpshooting program in 2007, a time point that coincides with the inflection in WI prevalence. Furthermore, it is estimated that for every 1% increase in clay, a 3.9% increase in CWD prevalence is expected (Walter et al., 2011). This information suggests expectations of higher prevalence in IL because of higher clay content compared to WI.

Relying on hunter harvest alone may be less effective at maintaining low CWD prevalence because, unlike government culling, there is no practical approach to concentrate hunter effort specifically in high risk CWD areas. Hunters take deer from a much larger area and do not target specific locales of high disease prevalence. In addition, animals often were located in areas where hunter harvest was not allowed and government culling represented the only avenue of control in those areas. Although hunter harvest was limited in the effect it had on CWD prevalence, hunter harvested deer were the primary mechanism for disease surveillance and serve a valuable role in early detection. Hunter surveillance and public reports of animals exhibiting clinical signs of CWD were used to find new positive locations. Once identified, the IDNR then focused culling efforts on these areas. Thus, the collaborative partnership between stakeholders and state agency personnel resulted in an effective control mechanism that incorporated early detection with localized disease management.

The use of government culling as a management strategy instead of increased public hunting has been criticized because of the perceived reduction in hunter opportunity (Holsman et al., 2010). Based on annual Illinois hunter harvest records, we found the Illinois disease management program has not had a negative effect on regional hunter harvest in northern Illinois. The number of deer harvested by hunters was greater in the 10 years since management began compared to the 10 years prior to disease management. While this may reflect additional hunting seasons that were created specifically to reduce herds in high risk areas, the increase in hunter harvest follows the same positive trajectory throughout the entire state of Illinois including areas where these additional seasons were not opened. At a smaller scale, two of the four Illinois counties that had the longest CWD management have seen

a reduction in hunter harvest, while two counties with the same length of management did not have a reduction in hunter harvest. Therefore, the impact of government culling on hunter opportunity is related to both the spatial scale at which harvest is measured and the spatial scale of the culling program. In Illinois, the state agency management program based on local culling likely has achieved the goal of preventing an increase in CWD without a consistent reduction of hunter opportunity at a local scale while also maintaining overall hunter opportunity at a larger scale throughout the state.

It is generally recognized that there are costs associated with either controlling wildlife disease or allowing the disease to run its course. Although not addressed by this study, it is likely the relative costs of these strategies are important in state agency management decisions. Public opinions are also important to wildlife management decisions because they can influence agency funding and support for management decisions. In the case of diseases such as CWD, the perceived threat of human health risks may influence public opinion of management decisions (Holsman et al., 2010). Because public perception of disease is tied to direct experiences (Camerer and Kunreuther, 1989), the absence of known associations of CWD with human neurological conditions (Belay et al., 2004) resulted in low perceived risk from consuming or handling infected tissues (Angers et al., 2006). This low risk perception may have translated into poor support for wildlife disease management.

Consideration of costs in wildlife disease management is further complicated by the potential of high future costs should new information indicate greater human health risks. Without disease management, CWD is likely to spread faster or farther. Increasing CWD prevalence or distribution in the present would make future disease control more difficult and expensive. According to models, an increase in CWD prevalence from 1 to 5% doubles the time required to have a 50% chance of eliminating the disease (Gross and Miller, 2001). Because complete eradication is unlikely, data driven management policies to contain disease spread are necessary for public support and economically justified to maintain herd health and future recreational opportunities (Gross and Miller, 2001; Saunders et al., 2012).

Previous disease models have provided inconsistent management recommendations because of a lack of empirical data on the role of density in transmission (Gross and Miller, 2001; Schaubert and Woolf, 2003; Wasserberg et al., 2009). A recent CWD model suggested focused culling is a more effective strategy for reducing CWD transmission compared to reducing overall deer numbers (Storm et al., 2013). Models suggest local culling is effective because cervid social group interactions are complex and variations in contact rates influence transmission (Habib et al., 2011; Potapov et al., 2013; Storm et al., 2013). Mateus-Pinilla et al. (2013) examined results of culling and concluded that frequent and continued culling is necessary to minimize CWD prevalence. The complexity of CWD transmission highlights the importance of standard reporting of CWD prevalence across states. We expect reliable data on this problem will significantly influence policy and CWD management decisions. Our comparison between states in this

study includes the longest sustained government culling program for wildlife disease in large mammals and is a unique opportunity to validate and improve models for disease control. We conclude that localized culling can maintain a low CWD prevalence in deer without compromising hunter harvest opportunities.

Conflict of interest statement

The authors declare no conflict of interest.

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References

- Almberg, E.S., Cross, P.C., Johnson, C.J., Heisey, D.M., Richards, B.J., 2011. Modeling routes of chronic wasting disease transmission: environmental prion persistence promotes deer population decline and extinction. *PLoS ONE* 6, e19896.
- Angers, R.C., Browning, S.R., Seward, T.S., Sigurdson, C.J., Miller, M.W., Hoover, E.A., Telling, G.C., 2006. Prions in skeletal muscles of deer with chronic wasting disease. *Science* 311, 1117.
- Barlow, N.D., 1996. The ecology of wildlife disease control: simple models revisited. *J. Appl. Ecol.* 33, 303–314.
- Belay, E.D., Maddox, R.A., Williams, E.S., Miller, M.W., Gambetti, P., Schonberger, L.B., 2004. Chronic wasting disease and potential transmission to humans. *Emerg. Infect. Dis.* 10, 977–984.
- Camerer, C.F., Kunreuther, H., 1989. Decision processes for low probability events: policy implications. *J. Policy Anal. Manage.* 8, 565–592.
- Carstensen, M., O'Brien, D.J., Schmitt, S.M., 2011. Public acceptance as a determinant of management strategies for bovine tuberculosis in free-ranging U.S. wildlife. *Vet. Microbiol.* 151, 200–204.
- Daszak, P., Cunningham, A.A., Hyatt, A.D., 2000. Emerging infectious diseases of wildlife – threats to biodiversity and human health. *Science* 287, 443–449.
- Gross, J.E., Miller, M.W., 2001. Chronic wasting disease in mule deer: disease dynamics and control. *J. Wildl. Manage.* 65, 205–215.
- Habib, T.J., Merrill, E.H., Pybus, M.J., Coltman, D.W., 2011. Modelling landscape effects on density–contact rate relationships of deer in eastern Alberta: implications for chronic wasting disease. *Ecol. Model.* 222, 2722–2732.
- Heberlein, T.A., 2004. Fire in the Sistine Chapel: how Wisconsin responded to chronic wasting disease. *Hum. Dimens. Wildl. Int. J.* 9, 165–179.
- Holsman, R.H., Petchenik, J., Cooney, E.E., 2010. CWD After the fire: six reasons why hunters resisted Wisconsin's eradication effort. *Hum. Dimens. Wildl.* 15, 180–193.
- Mateus-Pinilla, N.E., Weng, H.-Y., Ruiz, M.O., Shelton, P., Novakofski, J., 2013. Evaluation of a wild white-tailed deer population management program for controlling chronic wasting disease in Illinois, 2003–2008. *Prev. Vet. Med.* 110, 541–548.

- Mathiason, C.K., Hays, S.A., Powers, J., Hayes-Klug, J., Langenberg, J., Dahmes, S.J., Osborn, D.A., Miller, K.V., Warren, R.J., Mason, G.L., Hoover, E.A., 2009. Infectious prions in pre-clinical deer and transmission of chronic wasting disease solely by environmental exposure. *PLoS ONE* 4, e5916.
- Mathiason, C.K., Powers, J.G., Dahmes, S.J., Osborn, D.A., Miller, K.V., Warren, R.J., Mason, G.L., Hays, S.A., Hayes-Klug, J., Seelig, D.M., Wild, M.A., Wolfe, L.L., Spraker, T.R., Miller, M.W., Sigurdson, C.J., Telling, G.C., Hoover, E.A., 2006. Infectious prions in the saliva and blood of deer with chronic wasting disease. *Science* 314, 133–136.
- Miller, M.W., Williams, E.S., McCarty, C.W., Spraker, T.R., Kreeger, T.J., Larsen, C.T., Thorne, E.T., 2000. Epizootiology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. *J. Wildl. Dis.* 36, 676–690.
- Miller, M.W., Conner, M.M., 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: spatial, temporal, and demographic influences on observed prevalence patterns. *J. Wildl. Dis.* 41, 275–290.
- Peterson, M.J., 1991. Wildlife parasitism, science, and management policy. *J. Wildl. Manage.* 55, 782–789.
- Potapov, A., Merrill, E., Lewis, M.A., 2012. Wildlife disease elimination and density dependence. *Proc. R. Soc. B: Biol. Sci.* 279, 3139–3145.
- Potapov, A., Merrill, E., Pybus, M., Coltman, D., Lewis, M.A., 2013. Chronic wasting disease: possible transmission mechanisms in deer. *Ecol. Model.* 250, 244–257.
- Saunders, S.E., Bartelt-Hunt, S.L., Bartz, J.C., 2012. Occurrence, transmission, and zoonotic potential of chronic wasting disease. *Emerg. Infect. Dis.* 18, 369–376.
- Schauber, E.M., Woolf, A., 2003. Chronic wasting disease in deer and elk: a critique of current models and their application. *Wildl. Soc. Bull.* 31, 610–616.
- Schmitt, S.M., O'Brien, D.J., Bruning-Fann, C.S., Fitzgerald, S.D., 2002. Bovine tuberculosis in Michigan wildlife and livestock. *Ann. N.Y. Acad. Sci.* 969, 262–268.
- Spraker, T.R., Miller, M.W., Williams, E.S., Getzy, D.M., Adrian, W.J., Schoonveld, G.G., Spowart, R.A., O'Rourke, K.I., Miller, J.M., Merz, P.A., 1997. Spongiform encephalopathy in free-ranging mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*) and Rocky Mountain elk (*Cervus elaphus nelson*) in northcentral Colorado. *J. Wildl. Dis.* 33, 1–6.
- Storm, D.J., Samuel, M.D., Rolley, R.E., Shelton, P., Keuler, N.S., Richards, B.J., Van Deelen, T.R., 2013. Deer density and disease prevalence influence transmission of chronic wasting disease in white-tailed deer. *Ecosphere* 4, 1–10.
- United States Department of the Interior, 2011. National Atlas of the United States [WWW Document]. The Public Land Survey System (PLSS) <http://www.nationalatlas.gov/articles/boundaries/a.plss.html>
- VerCauteren, K.C., Hygnstrom, S.E., 2011. Managing white-tailed deer: Midwest North America. In: Hewitt, D.G. (Ed.), *Biology and Management of White-Tailed Deer*. CRC Press, Boca Raton, FL, pp. 517–518.
- Walter, W.D., Walsh, D.P., Farnsworth, M.L., Winkelman, D.L., Miller Michael, W., 2011. Soil clay content underlies prion infection odds. *Nat. Commun.* 2, 200.
- Wasserberg, G., Osnas, E.E., Rolley, R.E., Samuel, M.D., 2009. Host culling as an adaptive management tool for chronic wasting disease in white-tailed deer: a modelling study. *J. Appl. Ecol.* 46, 457–466.
- Williams, E.S., Miller Michael, W., Kreeger Terry, J., Kahn, R.H., Thorne, T., 2002. Chronic wasting disease of deer and elk: a review with recommendations for management. *J. Wildl. Manage.* 66, 551–563.
- Wisconsin's Chronic Wasting Disease Response Plan: 2010–2025, 2010.
- Woodroffe, R., 1999. Managing disease threats to wild mammals. *Anim. Conserv.* 2, 185–193.